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Crassisporium and *Romagnesiella*: two new genera of dark-spored Agaricales

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Abstract

A systematic study of a rare and enigmatic European species, *Galerina clavus* Romagn., is presented. Phylogenetic analyses show it to be most closely related to *Pachylepyrium carbonicola* (A.H. Sm.) Singer and *P. funariophilum* (M.M. Moser) Singer (Strophariaceae). Investigation of additional species of *Pachylepyrium* suggests this genus is polyphyletic as the type species, *P. fulvidula* (Singer) Singer, is nested in the Tubariaceae Vizzini based on multigene phylogenetic analyses. *Pachylepyrium nubicola* Singer is allied with *Pholiota* (Fr.) P. Kumm. based on high ITS similarity, and *P. carbonicola* and *P. funariophilum*, together with *G. clavus*, form a clade among a consortium of Strophariaceae Singer & A.H. Sm. and Hymenogastraceae Vittad. As a result, we propose *Romagnesiella* gen. nov. to accommodate *G. clavus*, for which a taxonomic description is given and lectotype and epitype are designated. The genus *Crassisporium* gen. nov. is proposed to encompass *Pachylepyrium funariophilum* (of which *P. carbonicola* is considered a younger taxonomic synonym), *P. chilense* M.M. Moser, and *P. squarrulosum* Singer. *Crassisporium* is distinguished from *Romagnesiella* by its thick-walled basidiospores and occurrence in burnt habitats. The identities of the morphologically similar *Tubaria umbonata* S. Lundell, *T. embolus* (Fr.) Sacc. and *T. minima* J.E. Lange are also discussed.

Key words

- Agaricoid clade,
- carbonicolous fungi,
- Hymenogastraceae,
- Pachylepyrium,
- Strophariaceae,
- taxonomy,
- taxon sampling,
- types

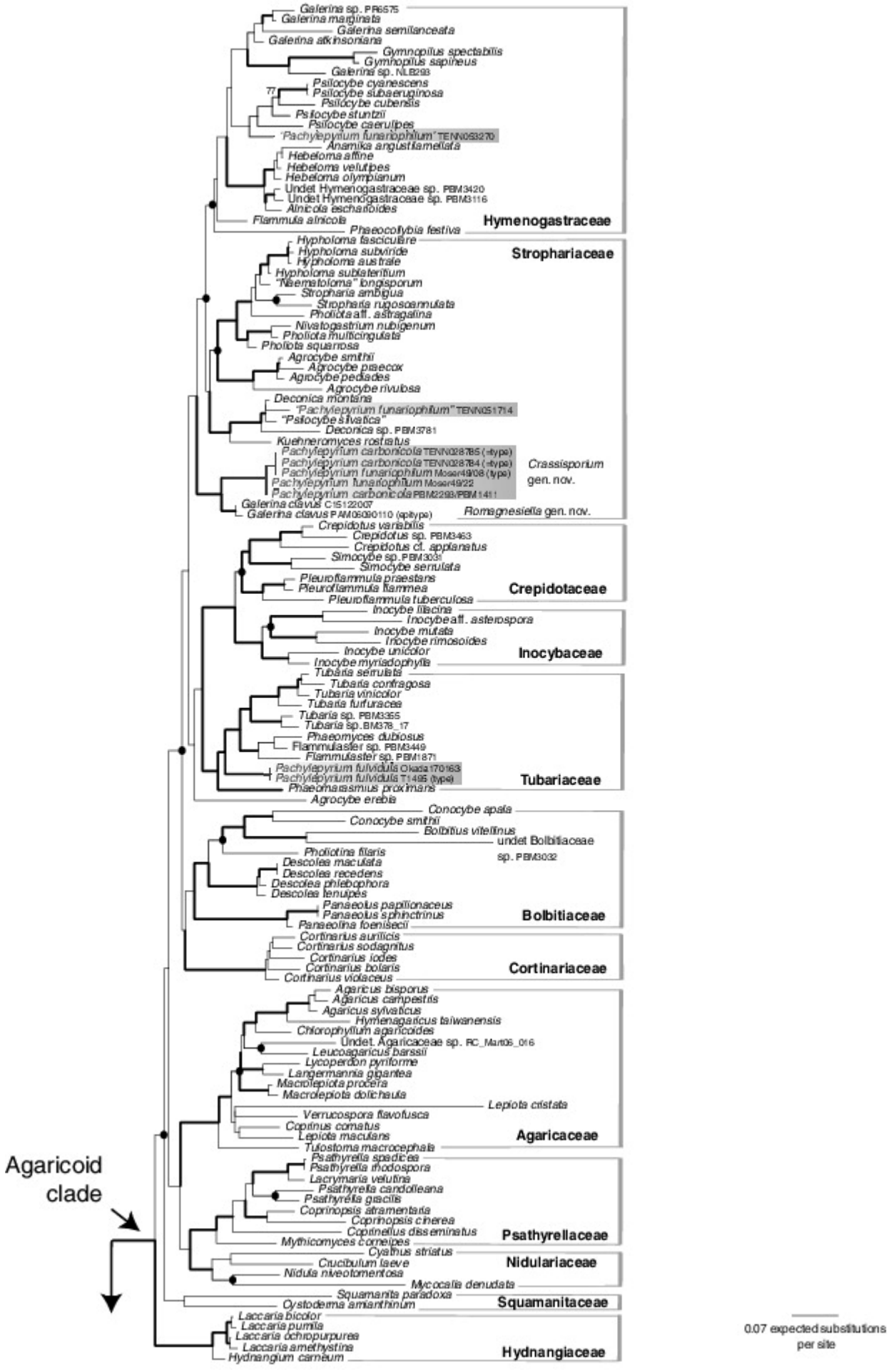
Introduction

Considerable progress has been made to assess phylogenetic relationships in the Agaricales (Binder, Larsson, Matheny, & Hibbett, 2010; Garnica, Weiss, Walther, & Oberwinkler, 2007; Matheny, et al., 2006; Moncalvo et al., 2002), the largest order of mushroom-forming fungi with some 13 500 described species (Kirk, Cannon, Minter, & Stalpers, 2008). However, continued assessment of evolutionary relationships within the order is necessary. For instance, taxa from the tropics and southern hemisphere are in need of better integration into more inclusive molecular systematic treatments (Matheny et al., 2009, Rees, Midgley, Marchant, Perkins, & Orlovich, 2013), and some species are known only from type collections, of insufficient age for adequate gene sampling, missing or unavailable (Ammirati, Parker, & Matheny, 2007; Baroni & Matheny, 2011).
The genus *Galerina* Earle (Agaricales), typified by *G. vittiformis* (Fr.) Singer, traditionally encompasses saprotrophic dark-spored agarics often with small and slender fruit bodies with a bell-shaped pileus (mycenoid or collybioid in habit), straight pileal margin, attached lamellae, presence of veil, and an ochre to rusty brown spore deposit. Spores of *Galerina* are typically yellow to dark tawny in KOH (potassium hydroxide), amygdaliform to elliptic, often verruculose or rugulose, and lack a well-defined germ pore. The spores of many species of *Galerina* are also characterized by a smooth region above the apiculus on the adaxial side of the spore (this is known as a plage) (Bon, 1992; Gulden, 2012; Watling & Gregory, 1993). The first (and only) detailed phylogenetic assessment of *Galerina* strongly suggests the genus is polyphyletic (Gulden, Stensrud, Shalchian-Tabrizi, & Kauserud, 2005).
Galerina clavus Romagn. (Fig. 1) is a small inconspicuous species published in 1944 by Romagnesi (1942) from Europe that displays a combination of anomalous characters for the genus: namely, its naucorioid habit (small size, pileus with a decurved margin), smooth spores without a plage, and absence of a veil. The combination of these traits cast doubts on an alliance with *Galerina* (de Haan & Walleyn, 2009; Moreau, 2009). Smith & Singer (1964) treated *G. clavus* in their world monograph of *Galerina* but placed it, together with the South American species *G. fuegiana* Singer, in an isolated section *Pseudotubaria* A.H. Sm. & Singer. This classification has been used by Bon (1992), Horak (2005), Moser (1978, 1983) and Singer (1986). Molecular systematic studies of *Galerina* and other dark-spored agarics (Aime, Vilgalys, & Miller, 2005; Garnica, Weiss, Walther, & Oberwinkler, 2007; Gulden, Stensrud, Shalchian-Tabrizi, & Kauserud, 2005; Matheny et al., 2006, 2007a; Moncalvo et al., 2002; Petersen, Knudsen, & Seberg, 2010; Walther, Garnica, & Weiß 2005) have not included *G. clavus*, and thus its systematic position remains ambiguous.
Fig. 1–2. Fruit bodies of *Galerina clavus in situ* (PAM06090110). Photo by P.-A. Moreau. Scale bar = 10 mm. (**Fig. 2**) Fruit bodies of *Pachylepyrium carbonicola* in situ (PBM2293, WTU). Scale bar = 10 mm. Photo by P.B. Matheny.

Based on preliminary phylogenetic analysis of nuclear ribosomal RNA (rRNA) gene sequences, samples of *G. clavus* clustered together with sequences of the North American species

Pachylepyrium carbonicola (A.H. Sm.) Singer (Fig. 2). The genus *Pachylepyrium* Singer (Agaricales, Strophariaceae; type: *P. fulvidula* (Singer) Singer), however, contains seven accepted species that differ from *G. clavus* by their thick-walled spores typically with a germ pore and presence of a veil. Furthermore, most species are carbonicolous (Claridge, Trappe, & Hansen, 2009; McMullan-Fisher et al., 2011), fruiting among burnt debris or on burnt ground in co-occurrence with bryophytes (viz. *Funaria* Hedwig) or on wood (lignicolous) (Moser, 2000; Singer, 1986). Thus, a substantial taxonomic emendation would be required to place *G. clavus* within *Pachylepyrium*.

Fig. 3. Phylogeny of the Agaricoid clade based on a Maximum Likelihood and Bayesian Inference analysis of a supermatrix of four nuclear gene regions (5.8S rRNA, LSU-rRNA, SSU-rRNA and rpb2 conserved domains 5–7). Thickened branches indicate ML bootstrap support >70% and Bayesian posterior probability >0.95. Nodes that receive Bayesian posterior probabilities >0.95 but with <70% ML bootstrap are indicated by small black-filled circles. Clade nomenclature follows Matheny et al. (2006). Grey shaded taxon labels indicate placement of species of *Pachylepyrium* or collections mislabelled *Pachylepyrium*.


Galerina sp. PR6575
Galerina marginata
Galerina semilanceata
Galerina atkinsoniana
Gymnopilus spectabilis
Gymnopilus sapineus
Galerina sp. NLB293
77
Psilocybe cyanescens
Psilocybe subaeruginosa
Psilocybe cubensis
Psilocybe stuntzii
Psilocybe caerulipes
'Pachylepyrium funariophilum' TENN053270
Anamika angustilamellata
Hebeloma affine
Hebeloma velutipes
Hebeloma olympianum
Undet Hymenogastraceae sp. PBM3420
Undet Hymenogastraceae sp. PBM3116
Alnicola escharoides
Flammula alnicola
Hymenogastraceae
Phaeocollybia festiva
Hypholoma fasciculare
Hypholoma subviride
Hypholoma australe
Hypholoma sublateritium
"Naematoloma" longisporum
Stropharia ambigua
Stropharia rugosoannulata
Pholiota aff. astragalina
Nivatogastrium nubigenum
Pholiota multicingulata
Pholiota squarrosa
Agrocybe smithii
Agrocybe praecox
Agrocybe pediades
Agrocybe rivulosa
Deconica montana
"Pachylepyrium funariophilum" TENN051714
"Psilocybe silvatica"
Deconica sp. PBM3781
Kuehneromyces rostratus
Pachylepyrium carbonicola TENN028785 (=type)
Pachylepyrium carbonicola TENN028784 (=type)
Pachylepyrium funariophilum Moser49/08 (type)
Pachylepyrium funariophilum Moser49/22
Pachylepyrium carbonicola PBM2283/PBM1451
Crassisporium gen. nov.
Galerina clavus C15122007
Galerina clavus PAM06090110 (epitype)
Romagnesiella gen. nov.
Strophariaceae
Crepidotus variabilis
Crepidotus sp. PBM3463
Crepidotus cf. applanatus
Simocybe sp. PBM3031
Simocybe serrulata
Pleuroflammula praestans
Pleuroflammula flammea
Pleuroflammula tuberculosa
Crepidotaceae
Inocybe lilacina
Inocybe aff. asterospora
Inocybe mutata
Inocybe rimosoides
Inocybe unicolor
Inocybe myriadophylla
Inocybaceae
Tubaria semilata
Tubaria confragosa
Tubaria vinicolor
Tubaria furfuracea
Tubaria sp. PBM3355
Tubaria sp. BM378_17
Phaeomyces dubiosus
Flammulaster sp. PBM3449
Flammulaster sp. PBM1871
Pachylepyrium fulvidula Okada170163
Pachylepyrium fulvidula T1495 (type)
Phaeomassmius proximans
Tubariaceae
Agrocybe erebia
Conocybe apala
Conocybe smithii
Bolbitius vitellinus
undet Bolbitiaceae sp. PBM3032
Pholiotina filaris
Descolea maculata
Descolea recedens
Descolea phlebophora
Descolea tenuipes
Panaeolus papilionaceus
Panaeolus sphinctrinus
Panaeolina foeniseci
Bolbitiaceae
Cortinarius aurilicis
Cortinarius sodagnitus
Cortinarius iodes
Cortinarius bolaris
Cortinarius violaceus
Cortinariaceae
Agaricus bisporus
Agaricus campestris
Agaricus sylvaticus
Hymenagaricus taiwanensis
Chlorophyllum agaricoides
Undet. Agaricaceae sp. RC_Mart05_016
Leucoagaricus barssii
Lycoperdon pyriforme
Langermannia gigantea
Macrolepiota procera
Macrolepiota dolichaula
Lepiota cristata
Verrucospora flavofusca
Coprinus comatus
Lepiota maculans
Agaricaceae
Tulostoma macrocephala
Psathyrella spadicea
Psathyrella rhodospora
Lacrymaria velutina
Psathyrella candolleana
Psathyrella gracilis
Coprinopsis atramentaria
Coprinopsis cinerea
Coprinellus disseminatus
Psathyrellaceae
Mythicomyces corneipes
Cyathus striatus
Crucibulum laeve
Nidularia niveotomentosa
Nidulariaceae
Mycocalia denudata
Squamanita paradoxa
Squamanitaceae
Cystoderma amianthinum
Laccaria bicolor
Laccaria pumila
Laccaria ochropurpurea
Laccaria amethystina
Hydnangium carneum
Hydnangiaceae
Agaricoid clade
0.07 expected substitutions per site

To confirm phylogenetic and taxonomic relationships to other species of *Pachylepyrium* (viz. the type species of the genus, *P. fulvidula*), we produced molecular data from four of seven type collections of species accepted in this genus. We also studied a fifth type collection morphologically and several collections of European naucorioid fungi showing similar characters to *G. clavus*, including *Tubaria umbonata* S. Lundell, *T. minima* J.E. Lange and *T. embolus* (Fr.) Sacc. Collections of *Pachylepyrium* are not common (Moser, 2000), probably owing to their specific habitat (mostly burnt areas), which is in decline in regions of Europe (Veerkamp 1998). While dense taxon sampling from broad geographic areas is a laudable goal, our focus is to produce a contemporary taxonomic revision based on available type materials. To accomplish this and a more thorough systematic comparison with *G. clavus*, we carried out a multi-gene phylogenetic analysis with an emphasis on the Agaricoid clade (Matheny et al., 2006) to investigate the relationship of *G. clavus* to *Pachylepyrium*.

Materials and methods

Morphological analysis

Collections of fruit bodies were studied from the personal herbarium of M. Contu and material preserved at IB, K, LIP, MICH, MPU, PC and TENN. Herbarium designations follow Thiers (continuously updated). Colour designations in the format '(5E7)' refer to plate, column and row of Kornerup & Wanscher (1967). Microscopic observations were made in 5% KOH, Melzer's reagent and water mounts. Spores were measured on a Moticam 1000 video camera connected to a Nachet Andromede 0181 compound microscope or on a Nikon Eclipse 80i using NIS Elements (D) imaging software. First and ninth deciles (D1, 9) and average values (italicized and in bold) are presented according to Fannechère (2005, 2009).

Type collections examined for molecular and taxonomic analyses

To evaluate the relationship between *Galerina clavus* and *Pachylepyrium*, we performed molecular and/or morphological annotations of five *Pachylepyrium* species, including type collections and the type species of the genus (*P. fulvidula*). The type of *G. clavus* is missing. *Pachylepyrium* types studied by us include: *P. carbonicola* AHS44640 (holotype of *Kuehneromyces carbonicola* A.H. Sm., MICH); *P. funariophilum* IB 1949/0008 (holotype of *Pholiotina funariophila* M.M. Moser); *P. nubicola* Singer K (M 181790) (holotype); *P. fulvidula* T1495 (isotype of *Phaeomarasmius fulvidulus*, MICH); and *P. chilense* M.M. Moser M3269 (paratype, MICH) (see also Appendix 1, online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2014.967823). We obtained a loan of part of the holotype (IB) of *P. chilense*, but the material was inadequate for destructive sampling. Material of representative *G. clavus* sequenced included PAM06090110 (LIP) and Contu 15122007 (pers. herb.). To assess the taxonomic relationship of *G. clavus* to *Tubaria umbonata* and *T. embolus*, we examined the isotype of *T. umbonata* (ex Fungi exsiccati Suecici 2041 (PC)) and accessions labelled as '*Galerina embolus*' (Fr.) P.D. Orton (Bon 741120, Bon 70624) at LIP. Other taxa selected for phylogenetic analyses are listed in Appendix 1 (see supplemental material online).

DNA extraction, PCR and Sanger sequencing

Procedures for DNA extraction, PCR and Sanger sequencing follow those outlined in Matheny et al. (2007b); Matheny, Austin, Birkebak, & Wolfenbarger (2010) except where mentioned below. For collections older than 30 years, we used an E.Z.N.A. High Performance (HP) Fungal DNA kit (Omega Bio-Tek, Norcross, Georgia, USA). We sampled the ITS region, including the 5.8S gene, using primers ITS1F and ITS4 (Gardes & Bruns 1993; White, Bruns, Lee, & Taylor, 1990); the 5′ end of the nuclear 25S large subunit ribosomal RNA gene region (nLSU) using primers LR0R and LR7 or LR5 (Vilgalys & Hester, 1990); almost the entire nuclear 18S small subunit ribosomal RNA gene (nSSU) between primers PNS1 and NS8 (O'Donnell, Cigelnik, & Benny, 1998; White, Bruns, Lee, & Taylor, 1990); and the most variable region of rpb2 between conserved domains 6 and 7 using primers b6F and b7.1R (Matheny, 2005). All new sequences have been deposited in GenBank (shown in bold in Appendix 1, see supplemental material online).

DNA alignments and phylogenetic analyses

We manually aligned 151 of our 153 new nLSU, nSSU, 5.8S and rpb2 sequences from 42 taxa, including type collections of *Pachylepyrium funariophilum* and *P. fulvidula* (type species of *Pachylepyrium*) with alignments produced by Matheny et al. (2006) in MacClade 4.08 (Maddison

& Maddison, 2005). We were only able to obtain ITS sequences from type collections of *Pachylepyrium nubicola* and *Pachylepyrium carbonicola*; thus, these were not added to our alignment due to insufficient variation across the 5.8S locus. Integration of ITS1 and ITS2 spacer sequences was not possible due to their high substitution rates. However, we did add sequences from two conspecific collections of *P. carbonicola* determined as such by A.H. Smith (sequences of which did not differ from the holotype). The datasets were pruned to exemplars of the Tricholomatoid clade and all members of the Agaricoid clade following Matheny et al. (2006). To these we added rRNA and/or rpb2 sequences of *Leucoagaricus barssii* (Zeller) Vellinga (Matheny et al., 2007b) and *Pseudoclitocybe cyathiformis* (Bull.: Fr.) Singer from Binder, Larsson, Matheny, and Hibbett (2010) and rRNA and/or rpb2 sequences of *Squamanita paradoxa* (A.H. Sm. & Singer) Bas, *Mycocalia denudata* (Fr. & Nordholm) J.T. Palmer and *Nidula niveotomentosa* (Henn.) Lloyd from Matheny & Griffith (2010). LSU and 5.8S sequences (AF261513, EF051055, EF051060) of '*Pachylepyrium funariophilum*' from Moncalvo et al. (2002) and '*Tubaria minima*' of Matheny et al. (2007a) were also added.

Alignments were concatenated in MacClade in a non-interleaved format with the final supermatrix composed of 170 taxa. Sixty-five taxa (38%) lacked rpb2 sequences, 21 (12%) lacked 5.8S sequences and 27 (16%) lacked SSU sequences. Several studies (Wiens, 2006; Wiens & Moen, 2008; Wiens & Tu, 2012) demonstrate that incorporation of incompletely sampled taxa in supermatrices improves phylogenetic accuracy, if the overall number of characters is sufficiently large, thus supporting a supermatrix approach. The concatenated alignment and tree files have been submitted to TreeBASE (S15353).

We converted the concatenated supermatrix from nexus format to a relaxed phylip format in Seaview version 4.2.4 (Gouy, Guindon, & Gascuel, 2010) after inspection for strongly supported conflict (>70%) between rRNA and rpb2 gene trees following Matheny (2005) using Maximum Likelihood (ML) bootstrapping as indicated below. The resulting concatenated rRNA and rpb2 phylip file contained 4508 total sites: 1451 sites from LSU, 1782 sites from SSU, 158 sites from the 5.8S gene and 1117 sites from the rpb2 gene region between conserved domains 5 and 7 after trimming staggered ends. A partition text file was created to model the rRNA gene regions (positions 1–3391) separately from first, second and third codon positions of rpb2 (positions 3392–4508) to allow separate GTRGAMMA models for each partition following model selection in Matheny et al. (2006) and recommendations made in the RAxML user manual (Stamatakis, 2006). Thus, four unique partitions were established with one for the rRNA gene regions and three separate partitions for each rpb2 codon position.

RAxML version 7.2.8 was used to generate 1000 rapid bootstraps and a final ML tree with all free model parameters estimated by the program. The same partitions were invoked using the parallel version of MrBayes 3.1.2 (Altekar, Dwarkadas, Huelsenbeck, & Ronquist, 2004; Ronquist & Huelsenbeck, 2003) for a Bayesian inference of the phylogeny with each partition modelled according to GTR+I+G following Matheny et al. (2006). This analysis entailed two independent runs for 50 million generations sampling trees and other parameters every 5000 generations on the Newton High Performance Computing cluster at the University of Tennessee. The average standard deviation of split frequencies was used as a metric to determine an appropriate burn-in. Trees were viewed in FigTree version 1.4.0 (Rambaut, 2009). *Pseudoclitocybe cyathiformis* was used for rooting purposes based on Binder et al. (2010). ML bootstrap proportions are referred to as MLBP and Bayesian posterior probabilities as BPP.

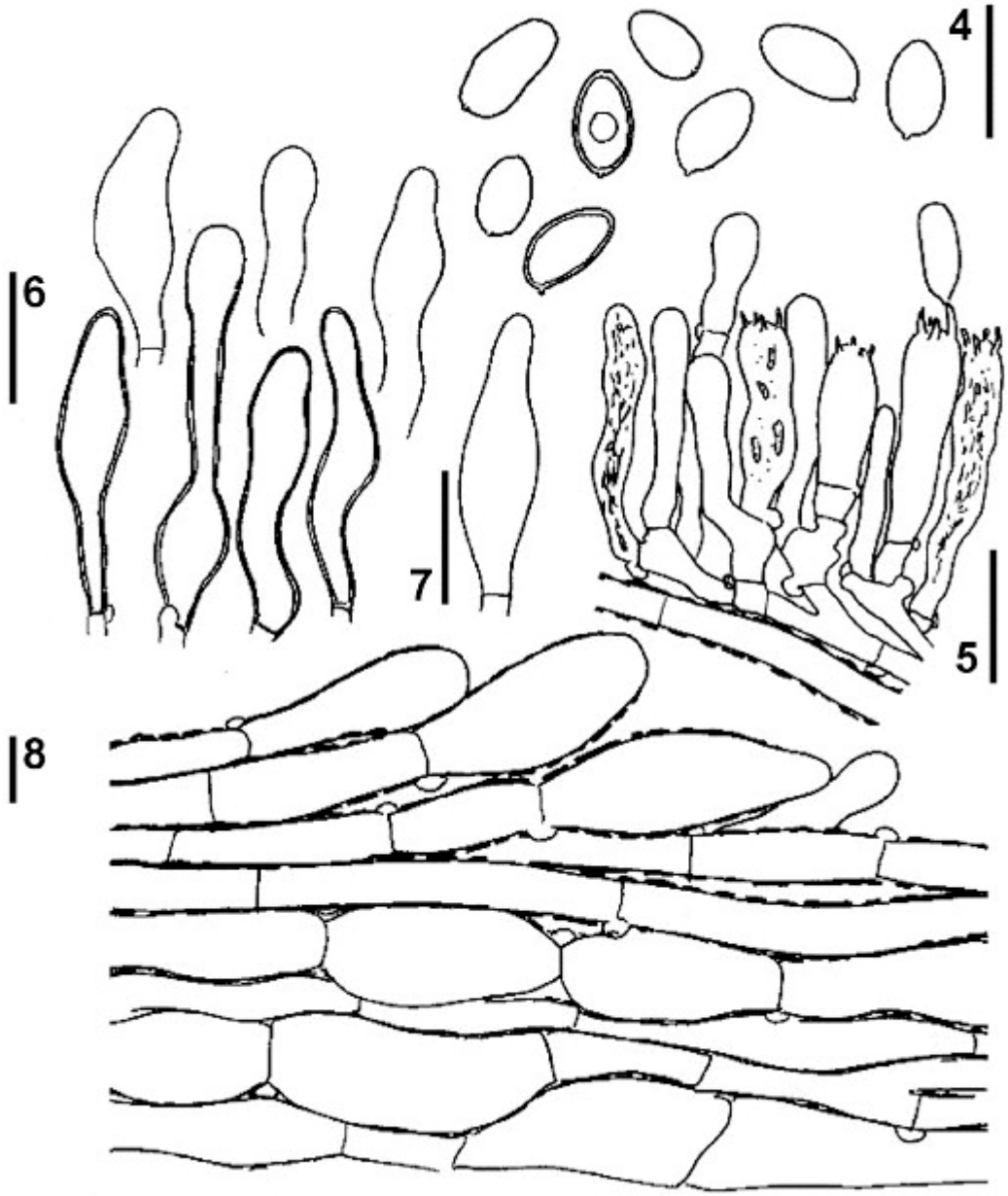
Results

Pachylepyrium is polyphyletic

152 ITS, 168 nLSU, 151 sSSU and 105 rpb2 sequences, 153 of which are new, were analysed for this study. The average standard deviation of split frequencies reached less than 0.01 by the 27 795 000th generation in the Bayesian inference analysis of the four-gene region supermatrix. We sampled trees every 5000 steps (producing a total of 10 001 trees for each of the two 50 million generation runs); thus, we conservatively burned the first 6001 trees, including the initial starting tree. Posterior probabilities were calculated from a total sample of 8000 trees (4000 from each run). Comparison of the rRNA-only ML phylogeny with that of the rpb2 ML phylogeny (data not shown) revealed no significantly supported conflicts.

The genus *Pachylepyrium* is polyphyletic (Fig. 3). The type species, *P. fulvidula*, clusters with strong support (80% MLBP, 0.99 BPP) among a grade of lineages that includes *Phaeomarasmius* Scherff., *Flammulaster* Earle and *Phaeomyces* E. Horak in the Tubariaceae. *Pachylepyrium carbonicola* and *P. funariophilum* cluster with strong support with *Galerina clavus* (90% MLBP, 1.0 BPP) forming a weakly supported sister group to exemplars of the Strophariaceae and Hymenogastraceae. ITS sequences of type collections of *Pachylepyrium carbonicola* and *P. funariophilum* differ only at two positions excluding polymorphic sites. A blastn analysis of the ITS sequence of the holotype of *Pachylepyrium nubicola* strongly suggests this species belongs to the genus *Pholiota* (96% similar to *Ph. terrestris* HQ604756, 95% similar to *Ph. gummosa* JF908581 and 95% similar to numerous other ITS sequences of *Pholiota*).

Figs. 4–8. Anatomical features of *Romagnesiella clavus* (PAM06090110, epitype). (**Fig.** 4) Spores. (**Fig.** 5) Basidia and subhymenium. (**Fig.** 6) *Cheilocystidia*. (**Fig.** 7) *Pleurocystidium*. (**Fig.** 8) Pileipellis. Scale bars = 10 μm.



Two collections (TENN053270, TENN05174) labelled *Pachylepyrium funariophilum* are incorrectly identified and not identical to each other. TENN053270, from Washington state, likely represents a species of *Psilocybe* as first suggested by Walther, Garnica, and Weiß (2005), whereas TENN051714, collected in North Carolina, is an unidentified species of *Deconica*. Morphological examination of both collections affirms these results.

The monophyly of the Agaricoid clade of Matheny et al. (2006) is for the first time highly supported (77% MLBP, 1.0 BPP). Monophyly of the Agaricoid clade was recovered with significant BPP in Garnica et al. (2007) and Matheny et al. (2006), but with poor maximum parsimony bootstrap support. The Hydnangiaceae is indicated as the sister group to the rest of the Agaricoid clade but with high BPP only (0.99). A grouping of the Cortinariaceae, Bolbitiaceae, Tubariaceae, Inocybaceae, Crepidotaceae, Strophariaceae, Hymenogastraceae, and *Agrocybe erebia* receives poor bootstrap support but high BPP (0.99). Taken together, eight of 12 families in the Agaricoid clade (Inocybaceae, Tubariaceae, Bolbitiaceae, Cortinariaceae, Agaricaceae, Psathyrellaceae, Nidulariaceae, Hydnangiaceae) receive strong statistical support in our analyses (MLBP >70% and BPP >0.95). The Hymenogastraceae and Crepidotaceae are supported with only high BPPs (0.99). The Squamanitaceae is recovered as monophyletic, but with poor support.

Similar to Matheny et al. (2006) the Hymenogastraceae and Strophariaceae are recovered as sister groups with a high posterior probability. Unlike Matheny et al. (2006) samples of *Gymnopilus*, which previously were placed in an isolated position with the Agaricoid clade, now cluster with samples of *Galerina* in the Hymenogastraceae but without strong support.
The lineage containing *Pachylepyrium funariophilum* and *P. carbonicola* is proposed as a new genus based on molecular, morphological and ecological distinctions between it and the lineage containing *Galerina clavus*, and due to the placement of the type of *Pachylepyrium* in the Tubariaceae. A separate genus is proposed to accommodate *G. clavus* due to differences in morphology and ecology with respect to *Pachylepyrium funariophilum* and *P. carbonicola*. All three taxa, however, are united by their basidiospores that darken to various shades of reddish brown in KOH. The spores of *Pachylepyrium fulvidula* are brownish yellow to yellowish brown in water mounts and darken to brown (not reddish brown) in KOH.

Taxonomy

Crassisporium Matheny, P.-A. Moreau & Vizzini gen. nov.
MYCOBANK No: MB 807853.
TYPE SPECIES: *Pholiotina funariophila* M.M. Moser, 1954.
ETYMOLOGY: crassus, Latin, means thick, and sporium, Latin, spore; in reference to the thick-walled basidiospores (gender: neuter).
DIAGNOSIS: Basidiomata naucorioid, pileus hygrophanous, veil present. Lamellae attached (adnate). Basidiospores smooth, ovate or subangular, wider in face view than in profile, thick-walled (>0.5 μm thick) and with a broad or conspicuous germ pore (often >0.5 μm wide), brownish yellow to golden yellow in water mounts, becoming rusty brown to reddish brown or rich reddish cinnamon in KOH. Pleurocystidia and chrysocystidia absent, cheilocystidia present. Pileipellis a cutis, not gelatinized. Hymenophoral trama regular to subregular, subhymenium not gelatinized. Clamp connections present. Carbonicolous. Typus: *Pholiotina funariophila* M.M. Moser, in Kühner & Romagnesi, Bull. Soc. nat. Oyonnax 8: 43, 1954.
Crassisporium chilense (M.M. Moser) Matheny, P.-A. Moreau & Vizzini, comb. nov.
MYCOBANK no: MB 807854.
BASIONYM: *Pachylepyrium chilense* M.M. Moser, Hoppea 61: 268, 2000, holotype seen. Chile.

Remarks

The carbonicolous habit and the smooth thick-walled basidiospores (*c*. 1.0 μm thick) with a distinct broad germ pore and rust brown colouration in KOH support transfer to *Crassisporium*. The species has been recorded from high-elevation (550 m) Nothofagus forests in Chile and differs from *P. funariophilum* by the somewhat smaller spores (7.0–8.5 × 4.5–6.0 μm versus 7.5–10.0 × 5.5–7.0 μm) and a more weakly developed and ochraceous veil, which is more strongly developed and white in *P. funariophilum* (Moser, 2000). Unfortunately, material sent to us from the holotype collection was not sufficient for examination and DNA extraction. However, upon examination of materials labelled *Pachylepyrium funariophilum* located at MICH, we found the spores of one collection (M3269, Validivia, Chile, including one small fruit body) to measure 7.0–8.5 × 4.5–6.0 μm. Based on the taxonomic key below, this material keys out to *Crassisporium chilense* due to the smaller spores and occurrence in Chile. Moser (2000) mistakenly cites two different collections (M3208 in the Latin diagnosis and M3269 in the German description) as the isotype of *Pachylepyrium chilense*. We suspect the designation of M3269 as isotype is an error as the referenced collection date (3 Mar. 1963) in Moser's publication does not match that for M3269 (31 Mar. 1963). Under this scenario M3269 is the paratype. Unfortunately, the collection date on the holotype packet (IB 1963/0210) is 30 Mar. 1963 (unlike the protologue), but the locality is exactly

that of M3269. Permission to extract DNA from the one small fruit body of M3269 (paratype) was not granted owing to the inadequate condition of this material.
Crassisporium funariophilum (M.M. Moser) Matheny, P.-A. Moreau & Vizzini, comb. nov. (Fig. 2, as *Pachylepyrium carbonicola*).
MYCOBANK No: MB 807855.
BASIONYM: *Pholiotina funariophila* M.M. Moser, in Kühner & Romagnesi, Bull. Soc. nat. Oyonnax 8: 43, 1954, holotype seen. Austria.
≡ *Pachylepyrium funariophilum* (M.M. Moser) Singer, in Singer & Moser, Mycopath. Mycol. Appl. 26(2-3): 171, 1965.
= *Kuehneromyces carbonicola* A.H. Sm., Beihefte zur Sydowia 1: 53, 1957. Holotype seen. Idaho.
≡ *Pachylepyrium carbonicola* (A.H. Sm.) Singer, Sydowia 11: 321, 1958 [1957].
≡ *Pholiota subangularis* A.H. Sm. & Hesler, The North American Species of Pholiota: 44, 1968.

Remarks

Crassisporium funariophilum is geographically widespread occurring in Europe, northern Africa and western North America (where it has been referred to as *Pachylepyrium carbonicola* and *Pholiota subangularis*) and may be expected elsewhere. Singer & Moser (1965) and Singer (1969) also report it from Argentina, but this material has not been revised in light of description of *P. chilense* (see above). Moser (2000) describes collections of *P. carbonicola* with a white fugacious veil and similar ecology to *P. funariophilum*, but with somewhat larger spores (8.2–12.1 × 6.5–8.3 μm) than for *P. funariophilum* (7.6–10.0 × 5.3–7.1 μm). However, pairwise comparison of ITS sequences from the type collections of *C. funariophilum* and *P. carbonicola* differ at only two nucleotide positions (excluding three polymorphic sites among the five sequences considered) strongly suggesting the two species are conspecific. As such, *P. funariophilum* has nomenclatural priority.
Crassisporium squarrulosum (Singer) Matheny, P.-A. Moreau & Vizzini, comb. nov.
MYCOBANK no: MB 807856.
BASIONYM: *Pachylepyrium squarrulosum* Singer, Beih. Nova Hedwigia 29: 281, 1969, holotype not seen. Chile.

Remarks

We have not studied material of *C. sqarrulosum*, but the thick spore wall with a truncate germ pore and intense ‘ferruginous’ colouration in KOH described by Singer (1969) are consistent with placement in *Crassisporium* rather than with the type of *Pachylepyrium* in the Tubariaceae or with *Romagnesiella*. The species is associated with burnt debris and occurs at high elevations (1000 m) in Chile. The type (M 6550) is reportedly at SGO. The species differs most readily from *C. chilense* by the flocculose-squarrose pileus surface and longer spores (12.0–14.0 × 6.5–8.0 μm).
Pholiota nubicola (Singer) Matheny & P.-A. Moreau, comb. nov.
MYCOBANK No: MB 807857.
BASIONYM: *Pachylepyrium nubicola* Singer in Dennis, Kew Bull. 15(1): 139, 1961, holotype seen. Venezuela.

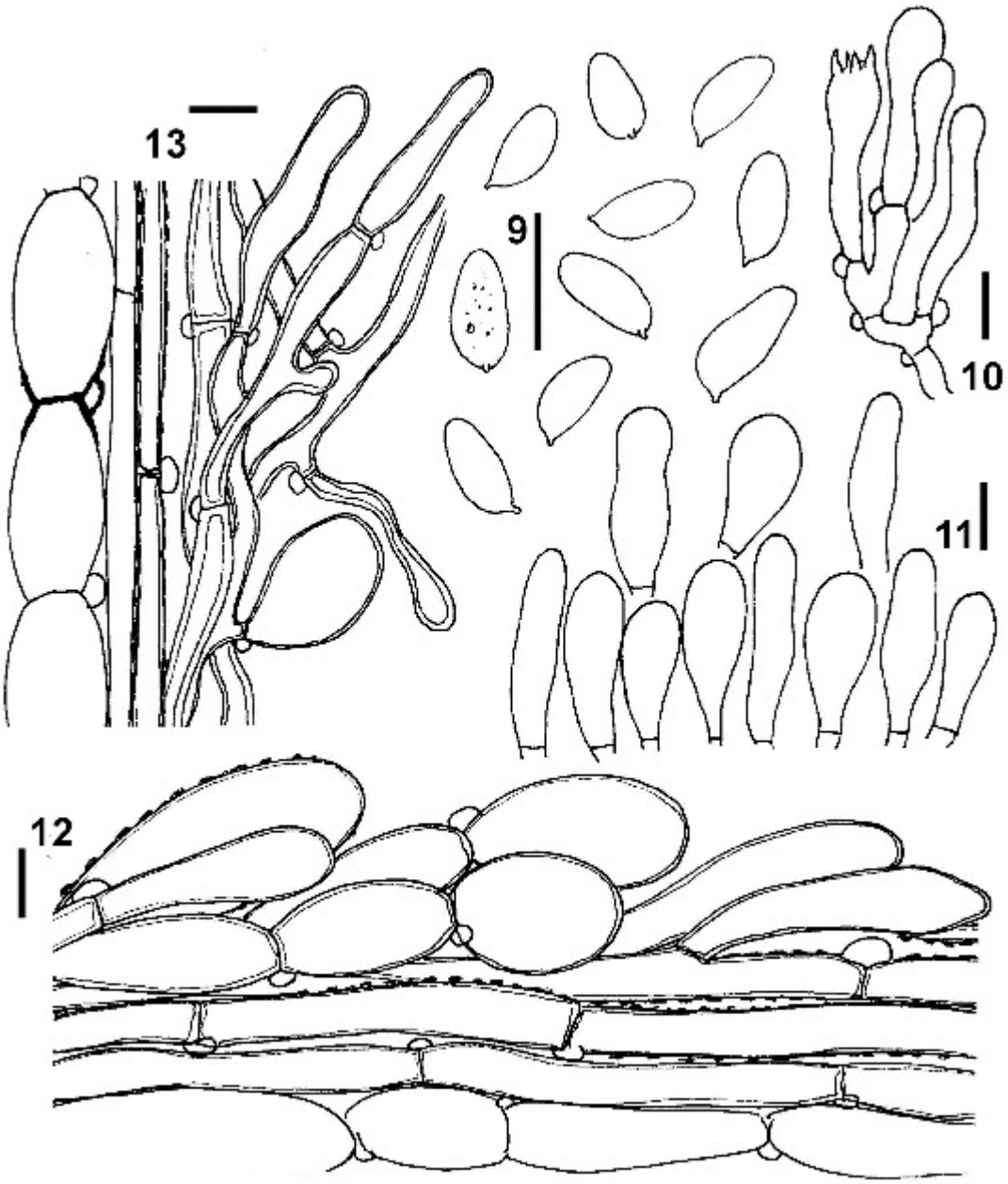
Remarks

The ITS sequence produced from the holotype strongly suggests that *Pachylepyrium nubicola* is a species of *Pholiota*. Consistent with this placement are the caespitose and lignicolous habit, paler (yellowish) pigmented basidiospores with a thinner wall than in *Crassisporium*, strongly gelatinized pileipellis composed of coarsely incrusted yellowish hyphae, and gelatinized subhymenial trama.

Add to this the slightly phaseoliform spores with a distinct germ pore (0.8–1.0 µm wide) and the squamulose stipe covering, it is not surprising *P. nubicola* would be closely related to *Ph. gummosa* (Lasch: Fr.) Singer as described by Holec (2001).
In contrast to the protologue, our examination of the type revealed a gelatinized pileipellis and cylindric to subphaseoliform non-dextrinoid basidiospores, these with a distinct germ pore. The spores measure 7.5–8.8 × 4.5–4.8 µm, which is consistent with the protologue. The basidia measure 17–28 × 7–8 µm with yellowish contents when mature. The lamellar edge was observed to be sterile and yellow but without reviving elements. The presence or absence of chrysocystidia could not be confirmed, but given the high sequence similarity to ITS sequences labelled *Ph. gummosa* and *Ph. terrestris*, we predict chrysocystidia will be found in this species.

A taxonomic key to species of *Crassisporium*

1(a) Pileus surface flocculose-squarrose, spores 12–14 × 6.5–8 µm….*C. squarrulosum* Singer
1(b) Pileus surface glabrous or with marginal fibrils, spores 7–11.5 × 5.5–7 µm…….2
2(a) Spores mostly 8–11.5 × 5.5–7 µm, in north temperate forests of Europe, North Africa and western North America (also reported from southern South America, but this is likely *C. chilense*); veil well developed, white……*C. funariophilum* (M.M. Moser) Singer
2(b) Spores mostly 7–9 × 4.5–6 µm, in *Nothofagus* forests in southern South America; veil weakly developed, ochraceous……*C. chilense* M.M. Moser
Romagnesiella Contu, P.-A. Moreau, Vizzini & A. de Haan, gen. nov.
MYCOBANK No.: MB 519559.
TYPE SPECIES: *Galerina clavus* Romagn., 1944 [1942].
ETYMOLOGY: named in honour of Henri Romagnesi, French mycologist (1912–1997) (gender: feminine).
DIAGNOSIS: Basidiomata naucorioid, lamellae distant, adnate to subdecurrent; pileus dry, not hygrophanus; stipe smooth, without a partial veil. Basidiospores smooth, more or less ovate, not subangular, yellow in water mounts, reddish ochre in KOH, not dextrinoid, germ pore absent; necrobasidia numerous; cheilocystidia present, edges of lamellae smooth and (sub)sterile, pleurocystidia present but dispersed and infrequent, pileipellis filamentous, hymenophoral trama regular, clamp connections frequent. On unburnt soil or sand among mosses and grasses. Typus: *Galerina clavus* Romagn., Bull. Trimest. Soc. Mycol. France 58(4): 149 (1944 [1942]).
Romagnesiella clavus (Romagn.) Contu, P.-A. Moreau, Vizzini & A. de Haan, comb. nov.
(Figs 1, 4–8).
Figs. 9–13. Anatomical features of *Tubaria umbonata* (Fungi Exsicatti Suecici fasc. 41–42, isotype). (**Fig.** 9) Spores. (**Fig.** 10) Basidia and subhymenium. (**Fig.** 11) *Cheilocystidia*. (**Fig.** 12) *pileipellis*. (**Fig.** 13) *Stipitipellis*. Scale bars = 10 µm.



MYCOBANK No.: MB 519560.
BASIONYM: *Galerina clavus* Romagn., Bull. Trimest. Soc. Mycol. France 58(4): 149, 1944 [1942], lectotype designated here (Fig. 14, p. 145, Romagnesi (1944) [1942], MBT177567); epitype designated here (P.-A. Moreau 06090110, LIP, MBT177568). Switzerland.
≡ *Naucoria clavus* (Romagn.) Kühner & Romagn., Fl. Anal. Champ. Sup.: 239 (1953, comb. inval., Art. 33.4).
MISAPPLICATIONS: *Tubaria minima* J.E. Lange sensu Moreau in Matheny et al. (2007a: 571); *Galerina embolus* (Fr.) Sacc. sensu Orton (1960: 239), sensu de Haan & Walleyn (2009: 64).
BIBLIOGRAPHY: Romagnesi (1942: 144, protologue); Kühner & Romagnesi (1953: 239; description); Smith & Singer (1964: 336); de Haan & Walleyn (2009: 64, 66: description, picture); North African collections: Hausknecht & Zuccherelli (1993: 47), Moreau (2009: 199).

Description

Pileus 5–9 (12) mm diam, hemispheric-umbonate then ± depressed around umbo, margin early inrolled becoming shortly crenulate when old, even, not striate, densely furfuraceous-micaceous, grey-brown with somewhat purplish tones when fresh, paler at margin, quickly fading from margin to uniformly fleshy-ochre, without any trace of veil. Lamellae adnexed-ventricose at first, becoming shortly uncinate in age, distant with 14–16 L reaching stipe, interspersed by 1–2 series of lamellulae, dull rusty ochre even when young; edges smooth but (sub)sterile, pale yellow. Stipe 15–25 × 1 mm, flexuose, slightly attenuate at base and inflated at apex, pruinose-floccose just below lamellae, fibrillose below then glabrous against a uniform dirty brown ground colour, slightly purplish when young; no perceptible trace of veil (primordia not observed). Context dark brown when fresh, pale ochre when dry. Odour and taste fungoid, not remarkable.
Basidiospores (5.6) 6.2–6.7–7.3 (8.5) × (3.6) 3.9–4.2–4.4 (5.0) μm, Q = 1.51–1.62–1.73 (n = 48), ovate to obovate but longer spores more fusiform, smooth, germ pore absent; bright yellow in water, amber yellow in Melzer's, warm reddish ochre in KOH, wall thickened up to 0.3 (0.5) μm; content with a large central droplet, often elongate. Basidia four-spored, 28–36 × 7–9 μm, broadly clavate, with long sterigmata, content often microguttulate; necrobasidia abundant, with reddish-brown content. Cheilocystidia 22–45 × 5.5–7 μm, cylindrical-flexuose with slightly thickened yellowish wall, mixed with fascicles of terminal hyphae issued from trama with pear-shaped to subglobose terminal cells, 9–14 μm wide, lamella edge fertile to locally substerile. Pleurocystidia 38–42 × 7.5–13 μm, cylindrical to subutriform, not very distinct but not rare. Hymenophoral trama regular, with strongly encrusted hyphae, 3–5 μm wide. Pileipellis a superficial layer of short cells, these lobate, digitate, puzzle-like, fusiform or pyriform, 12–16 μm wide, more or less erected to nearly hymeniform towards margin, pale in KOH, smooth, issued from hyphae of subpellis; subpellis filamentous, coarsely encrusted, thick-walled, deep yellow to reddish brown in KOH, continuous with pileus context. Stipitipellis a cutis with sparse to fasciculate (at apex) caulocystidia measuring 16–25 × 5–12 μm, cylindrical to clavate-pyriform, very rare below apex; superficial hyphae slender, 2–3.5 μm wide. Clamp connections frequent.
Habitat and distribution: Often on calcareous, mineral-rich, sandy or alluvial substrates in pioneer or disturbed habitats including fixed coastal dunes and banks of trails or paths among mosses and grasses. Less frequent in secondarized dunes, scattered and never abundant. Europe (Belgium, France, Switzerland) and reported from Italy, the Netherlands, and North Africa. Fruiting Sept.–Nov.
Material studied: BELGIUM. Antwerpen: Antwerpen-Linkeroever, Het Rot, 4 Sep 2004; 10 specimens, among grass and mosses (*Tortula ruralis* and *Ceratodon purpureus*) on sandy, calcareous soil, herb. A. de Haan n° 04101; Antwerpen-Linkeroever, Blokkersdijk, 9 Sep 2004, 2 specimens, among mosses on sandy, calcareous soil, herb. A. de Haan n° 04113. Namur: Oignies-en-Thièrache, l'Estache, 23 Sep 1999, 1 specimen on wet calcareous soil, herb. A. de Haan n° 99100. Oost-Vlaanderen: Zwijnaarde, Rijvisschepark, 15 Oct 1989, about ten carpophores, in bare spot in mossy lawn, on sandy slightly loamy soil, leg. P. Van der Veken, herb. A. de Haan n° 89017; same location, leg. P. Van der Veken, 4 specimens, 29 Oct 2003, herb. A. de Haan n° 03088. West-Vlaanderen: De Panne, Calmeijnbos, 3 Nov 1997, 4 specimens, on humus-rich, calcareous soil, herb. A. de Haan n° 97088; Oostduinkerke, Doornpanne, 1 Nov 2001, 2 specimens, among moss and lichens, on calcareous dune sand, herb. A. de Haan n° 01080 (as '*Galerina embolus*'). FRANCE. Pas-De-Calais: Equihen-Plage, dunes d'Ecault, 7 November 2004, five specimens in Phleo-Tortuletum with *Calamagrostis epigeos*, calcareous fixed dune, leg. A. Brabant & P.-A. Moreau, 7 Nov 2004, herb. P.-A. Moreau n° 04110710 (LIP); same location, along a sandy path amongst *Calamagrostis epigeos*, fixed calcareous dunes with *Hippophae rhamnoides*, leg. C. Hannoire & P.-A. Moreau, 31 Oct 2008, herb. P.-A. Moreau n° 08103102 (LIP). Seine: Paris, bois de Vincennes, 1 Oct 1932, herb. R. Kühner (G, as '*Tubaria oligophylla*', ined.). ITALY: Sardinia, prov. Olbia, Golfo Aranci, Golfo di Marinella, in troops on sandy soil in a coastal grassland, leg. M.

Contu, 15 Dec 2007, herb. M. Contu (C15122007, TENN 063957). SWITZERLAND. Gräubunden: Rothenbrunnen, edge of path, riparian *Alnus incana* forest, on black alluvial humus, 1 Sep 2006, leg. B. Senn-Irlet & P.-A. Moreau, herb. P.-A. Moreau n° 06090110 (epitype LIP), TENN 063587, TENN 063976.

Remarks

Our interpretation of *Galerina clavus* is based on the detailed protologue of Romagnesi (1944 [1942]), which matches collections from Belgium and Switzerland. Unfortunately, no original material of *Galerina clavus* exists. The herbarium packet corresponding to one of the two collections cited by Romagnesi (1942: 145) Yerres, bois de Cerçay, 18 Jun 1942, kept in herb. H. Romagnesi (PC) was empty. The other cannot be located. Because a figure that depicts *G. clavus* exists in the protologue, this must serve as the lectotype. Original drawings of *G. clavus* made by Romagnesi also exist at PC. Thus, we designate PAM06090110 (LIP) as an epitype.
The species features some morphological and microscopic variation. The epitype (sequenced here), showed purplish-grey tones on the stipe as well as the pileus, but the protologue only mentions this colour on the stipe. Belgian collections described by de Haan & Walleyn (2009) describe a more convex pileus, broadly adnate instead of subdecurrent lamellae, a 'weakly farinaceous' taste, and habitat in dry mineral spots in urban grasslands. However, all collections show gradual variation in the pileus shape, colour and lamellae attachment.
Coastal collections are probably better considered as variants of *R. clavus*. Despite some variation in spore dimensions we could not find any support for specific or infraspecific distinctions. Detailed spore measurements illustrate continuity in these variation patterns but apparent differences (Appendix 2, see supplemental material online).
North African and Sardinian collections of *Galerina clavus*, as described by Hausknecht & Zuccherelli (1993) and Malençon (Moreau, 2009), differ from continental collections by somewhat larger basidiospores [(7.0) 7.6–8.2–9.0 (10) × (4.0) 4.9–5.2–5.5 (5.7) µm, Q = 1.48–1.59–1.70], slightly larger cystidia, and a filamentous pileipellis with a more or less continuous suprapellis of slender cylindrical hyphae with sparse slightly upraised terminal elements. It is possible that Mediterranean collections may represent distinct populations. One collection from Sardinia was sequenced (C15122007, leg. M. Contu), in which the ITS1 region reveals nine site differences with *R. clavus* PAM6090110, four of which, however, are polymorphic in C15122007. *Galerina clavus* has also been reported from the Netherlands (www.verspreidingsatlas.nl/046620).
Romagnesiella clavus is probably often confused with other naucorioid species frequent in the same environment, such as *Galerina graminea* (Velen.) Kühner, *Psilocybe pratensis* P.D. Orton, or *Tubaria* spp. The distant lamellae and absence of a veil on the stipe are good distinctive field characters. However, we discuss below three additional species with which *R. clavus* could be confused.
Tubaria umbonata S. Lundell in Lundell & Nannfeldt (1953: 23).
(Figs 9–13).
MYCOBANK No. 307168.
ISOTYPE: SWEDEN. Upland: Uppsala, Slottsbaken, NW part below Gunillaklaken, 50 m from Stockholmsvägen, 6 August 1944, leg. S. Lundell, ex Fungi exsiccati Suecici 2041 (PC, about 20 well-preserved specimens).

Description

Exsiccata small to minute (2–6 mm), very slender, entirely dark brown, without visible veil, with arcuate and distant lamellae. Basidiospores (6.2) 6.5–7.2–8.0 (9.0) × (3.0) 3.2–3.7–4.2 µm, Q = 1.70–1.96–2.24 (n = 23; see also Appendix 2, see supplemental material online), pale yellow, slightly thick-walled (<0.5 µm thick), ochraceous yellow in KOH, not collapsing, narrowly ovo-ellipsoidal to ellipsoidal, with slightly guttulate content, not dextrinoid. Basidia 22–34 × 6.5–7.5 µm, 4-spored (occasionally 2-spored), clavate more or less capitate, often strangulate under apex before maturity, hyaline; subhymenium 12–15 µm thick, filamentous-ramose, with hyphae 2–2.5 µm wide. Cheilocytidia 16–30 × 6–11.5 µm, often clustered–ampullaceous, clavate, ellipsoidal, utriform, cylindrical, with a thin and smooth wall, intermixed with some fertile basidia; lamella edge almost sterile. Pleurocystidia if present, not studied. Hymenophoral trama regular, yellowish, made of slender hyphae 2–6 µm wide with thick encrusted wall. Pileipellis with a discontinuous suprapellis made of +/− erected wide ellipsoidal to cylindrical catenulate elements, 18–30 × 6–13 µm, pale, slightly thick-walled, not or only locally encrusted; subpellis made of slender hyphae 3.5–8 µm wide, distinctly encrusted by granular pigment remaining yellow in KOH. Stipitipellis with sparse traces of filamentous veil towards apex, composed of slender hyphae 3–5 µm wide; wall yellowish, up to 2 µm thick and encrusted, terminal cells cylindrical with some vesicular cells up to 20 µm wide; superficial hyphae slender, these 3–5 µm wide, with yellow walls up to 0.5 µm thick, intermixed with large cylindrical hyphae 9–16 µm wide, locally encrusted by gold-yellow pigment (KOH), especially at septa, and some sparse pale gleoplerous hyphae. Clamp connections present at septa.

Remarks

Tubaria umbonata has not been revised nor documented since its publication in Fungi Exsiccati Suecici (Lundell & Nannfeldt 1953). We studied the isotype at PC (Fungi Exsiccati Suecici fasc. 41–42). Based on our morphological analysis, we conclude that *T. umbonata* represents a genuine species of *Tubaria* (W.G. Sm.) Gillet, but with rather narrow spores. DNA extraction of the PC material of *T. umbonata* yielded no PCR amplicons. Illustrations of anatomical features (Fig. 5) and their description (above) from the isotype are presented.

Two additional species could be confused with *R. clavus*. The name *Tubaria minima* J.E. Lange (Lange, 1940) was misapplied by Moreau (in Matheny et al., 2007a) to collections of *R. clavus*. Although Bon (1992) maintains *T. minima* as an autonomous species, Romagnesi (1942) considers it to be a synonym of *T. minutalis* Romagn. (Romagnesi, 1937), a position followed by modern authors. This species (sensu Lange (1940), non Moreau) differs from *G. clavus* by its hygrophanous piles and smaller spores (5.2–6.0 × 3.2–3.8 µm), features that reinforce its conspecificity with *T. minutalis*.

Tubaria embolus (Fr.) Sacc. is rather frequently cited in the literature but has been interpreted several different ways. Lange (1938: 655, pl. 127B) illustrates as '*Tubaria embola*' a species with broadly adnexed lamellae and yellow tones especially in the context (conforming to Fries' protologue, 1836–1838: 206), which seems to represent *Agrocybe pusiola* (Fr.) R. Heim. Bon (1992) cites the species in the genus *Galerina*, but examination of his materials (LIP) showed that his concept was unclear: coll. 741120 is *Galerina uncialis* (Britzelm.) Kühner, and coll. 70624 (as '*Galerina* cf. *embolus*') is a species with pleurocystidia close to *Galerina vittaeformis* (Fr.) Kühner. Orton (1960: 176) mentions five reports of *T. embolus* (as '*Galerina embolus*') from sand dunes, with comparable microscopical characters (but with notably long spores, 9–11 × 4.5–6 µm, compatible with our coastal collections of *R. clavus*), but pleurocystidia and necrobasidia are not mentioned. Moreover, yellow tones are described towards the pileus margin when dry, incompatible with any species known to us. In addition de Haan & Walleyn (2009) describe without illustrations

a collection of *G. embolus* (reported here as *R. clavus*) and also found in fixed dunes in Belgium. Considering the ambiguities of the protologue (Fries, 1836–1838), and the diversity of interpretations proposed by various authors, we reject the name here. Additional morphological and molecular study is required to unravel the taxonomic relationships of these variously interpreted collections to Romagnesiella.

Discussion

Polyphyly of *Pachylepyrium* and recognition of *Crassisporium* and *Romagnesiella* as new genera

Our results strongly support the polyphyletic status of *Pachylepyrium*. The type species of the genus, *P. fulvidula*, lacks several of the features attributed to the residual species. Originally described in *Phaeomarasmius*, *P. fulvidula* fruits on non-burnt woody debris and lacks the broad germ pore observed in other species. Horak (1968) reports seldom seeing any germ pore at all in the type of *P. fulvidula*. Our examination of the isotype at MICH confirms this observation (a germ pore was not observed). Thus, it is not surprising to see phylogenetic placement of *P. fulvidula* apart from the residual *Pachylepyrium* species. *Pachylepyrium fulvidula* resides in the Tubariaceae (Fig. 3) where it is closely related to other species of *Flammulaster*, *Phaeomyces*, *Phaeomarasmius* and *Tubaria* (W.G. Sm.) Gillet, all of these also lacking a broad germ pore (Horak, 2005).
We place three residual species of *Pachylepyrium* in the new genus *Crassisporium* united by a combination of basidiospore features (thick-walled spores with a broad germ pore and rusty to reddish brown colouration in KOH), anatomical features (non-gelatinous cutis, absence of pleurocystidia and chrysocystidia, absence of a gelatinous subhymenial layer) and ecology (carbonicolous habit). However, before our phylogenetic analysis based on molecular data, we did not suspect that *Galerina clavus* would be related to *Crassisporium* more so than to any other group of Hymenogastraceae or Strophariaceae. In order to point out differences between typical carbonicolous species with thick-walled pored spores (*Crassisporium* species) and non-carbonicolous species with thinner-walled (<0.5 μm) spores such as *G. clavus*, we have proposed a new genus *Romagnesiella* to accommodate the latter. No extra-European or North African species are unequivocally attributable to *Romagnesiella* at present without the addition of detailed morphological and molecular study. *Galerina fuegiana* Singer from Patagonia (Smith & Singer, 1964) is a possible candidate.
The inclusion of sequences of *Crassisporium* and *Romagnesiella* in a multigene phylogenetic analysis of the Agaricoid clade shows these two taxa form a well-supported group (Fig. 3) sister to the Strophariaceae s.lat. consortium (Gulden et al., 2005), including the families Hymenogastraceae and Strophariaceae s. str. of Matheny et al. (2006). Inclusion of *Crassisporium* and *Romagnesiella* in Strophariaceae s. str. would render the family paraphyletic in this analysis. Consideration of a more broadly conceived Hymenogastraceae, subsuming the Strophariaceae, could be made since the name Hymenogastraceae Vitt. 1831 pre-dates that of the Strophariaceae Singer & A.H. Sm. 1946. However, additional taxon and gene sampling are needed to resolve the relationship between these two families.
An alternative scenario to consider is inclusion of the three species of *Crassisporium* into one genus with *R. clavus*, thereby describing only a single genus as new. Samples of each group form a clade with strong support, a synapomorphy of which are the basidiospores that deepen various shades of reddish brown in KOH. However, we favour separate genera for the two lineages for several reasons: (1) species of *Crassisporium* are carbonicolous, whereas those of *Romagnesiella* are non-carbonicolous; (2) the lamellae are adnate to subdecurrent in *Romagnesiella* but never subdecurrent

in *Crassisporium*; (3) a veil is absent in *Romagnesiella* but present in *Crassisporium*; (4) the basidiospores of *Crassisporium* feature walls >0.5 µm thick, a wide germ pore typically 1.0–1.5 µm thick, and are subangular in face view. These features may be correlated with the fire ecology in that heat may be required to induce germination (Claridge, Trappe, & Hansen, 2009). Basidiospores of *Romagnesiella* have thinner walls (<0.5 µm thick), no germ pore and are not subangular; (5) pleurocystidia are present in *Romagnesiella* but absent in *Crassisporium*; and (6) the relative branch length differences between the two lineages correspond to branch length differences between other genera of Strophariaceae and Hymenogastraceae. Therefore, we prefer to recognize the two lineages as separate genera.

The monophyly of the Agaricoid clade is recovered here for the first time with high bootstrap and significant Bayesian posterior probability. Most species in the Agaricoid clade tend to have pigmented and thick-walled spores, perhaps indicative of adaptations to novel environments (e.g. dung, burnt sites) (Garnica et al., 2007). Many species of the Agaricoid clade also feature multiple nuclei per spore and an open pore type of hilum (Matheny et al., 2006).

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Supplemental data

Appendix 2. Table of basidiospore measurements from collections of *Romagnesiella clavus* and *Tubaria umbonata*.

Specimen-Voucher	No. of spores measured	Length (µm)	Width (µm)	Q
R. clavus	Not provided	7.5-10.0	4.0-5.0	Not provided
Romagnesi 1942: 145				
R. clavus Kühner	10	6.8-***7.2***-8.0	4.0-***4.5***-4.8	1.51-***1.61***-1.71
R. clavus PAM06090110 (neotype)	48	(5.6-) 6.2-***6.7***-7.3 (-8.5)	(3.6-) 3.9-***4.2***-4.4 (-5.0)	1.51-***1.62***-1.73
R. clavus AdH99100	30	(6.5-) 6.7-***7.4***-8.0 (-8.2)	(3.6-) 3.9-***4.2***-4.6 (-4.7)	1.59-***1.76***-1.95
R. clavus AdH03088	30	(6.9-) 7.4-***7.9***-8.7 (-9.1)	(4.1-) 4.2-***4.5***-4.8 (-5.3)	1.59-***1.75***-1.93
R. clavus AdH89017	30	(7.2-) 7.4-***8.0***-8.5 (-9.7)	(4.2-) 4.4-***4.7***-5.1 (-5.3)	1.53-***1.69***-1.86
R. clavus PAM08103102	57	(6.7-) 7.1-***8.0***-9.1 (-10.0)	(3.9-) 4.1-***4.4***-4.7 (-4.9)	1.64-***1.84***-2.05
R. clavus AdH97088	30	(7.1-) 7.4-***8.1***-8.6 (-10.3)	4.7-***5.0***-5.3 (-5.4)	1.50-***1.62***-1.72

R. clavus PAM04110710	48	(6.5-) 7.0-***8.2***-9.4 (-10.2)	(4.1-) 4.5-***4.9***-5.3 (-5.5)	1.47-***1.69***-1.89
R. clavus AdH04101	30	(7.5-) 7.9-***8.4***-8.9 (-10.3)	(4.1-) 4.5-***4.8***-5.1 (-5.5)	1.64-***1.77***-1.88
R. clavus AdH04113	30	(7.6-) 8.0-***9.0***-9.9 (-10.1)	(4.6-) 4.7-***5.0***-5.3 (-5.6)	1.67-***1.81***-1.96
R. clavus AdH78133	30	(8.1-) 8.5-***9.4***-10.3 (-10.5)	(4.6-) 4.7-***5.0***-5.5 (-5.8)	1.74-***1.86***-1.98
R. clavus AdH01080	30	(6.9-) 7.3-***8.1***-9.2 (-10.7)	(4.3-) 4.4-***4.7***-5.0 (-5.7)	1.53-***1.69***-1.89
Tubaria umbonata (holotype)	20	(6.2-) 6.5-***7.2***-8.0 (-9.0)	(3.0-) 3.2-***3.7***-4.2	1.70-***1.96***-2.24

Species	***Specimen-voucher***	***Locality***	***GenBank accession numbers***			
			ITS	nLSU	nSSU	*rpb2*
Agaricus bisporus	RWK1885	Denmark	DQ404388	AY635775	AY787216	AF107785
Agaricus campestris	TENN062420	Massachusetts, USA	DQ486682	DQ110871	DQ113914	
Agaricus sylvaticus	JFM-AS	Taiwan	AJ244523	AJ244523	AJ012405	
Agrocybe erebia	TENN062767	Massachusetts, USA	DQ484056	DQ457663	DQ440631	DQ472712
Agrocybe pediades	PBM2080 (WTU)	California, USA	DQ484057	DQ110872	DQ113915	
Agrocybe praecox	PBM2310 (WTU)	Washington, USA	AY818348	AY646101	AY705956	DQ385876
Agrocybe rivulosa	**TENN068272**	**Tennessee, USA**	**KF830098**	**KF830090**	**KF830078**	**KF830069**
Agrocybe smithii	PBM2298 (WTU)	Washington, USA	DQ484058	DQ110873	DQ115779	
Alnicola escharioides	PBM1719 (WTU)	Washington, USA	AY90086	AY380405		AY337411
Anamika angustilamellata	HKAS42927	China	AY575919	AY575919	DQ092918	
Asterophora lycoperdoides	CBS170.86	Unknown	AF357037	AF223190	DQ367417	DQ367431
Bolbitius vitellinus	MTS5020 (WTU)	Washington, USA	DQ200920	AY691807	AY705955	DQ385878
Callistosporium graminicolor	PBM2341 (WTU)	Washington, USA	DQ484065	AY745702	AY752974	DQ825406
Calocybe carnea	CBS552.50	France	AF357028	AF223178	DQ367418	DQ367432
Calocybe gangraenosa as "*Lyophyllum leucophaeatum*"	HAe251.97	Unknown	AF357032	AF223292	DQ367420	DQ367434
Catathelasma ventricosum	PBM2403 (WTU)	Oregon, USA	DQ486686	DQ089012	DQ435811	DQ470830
Chlorophyllum agaricoides	RWK Sa1	Greece	DQ200928	AY700187	AY657010	
Cleistocybe carneogrisea	TENN063842	France	HQ728526	HQ728527	HQ728528	
Cleistocybe vernalis	PBM1856 (WTU)	Washington, USA	DQ486692	AY647208	DQ092913	
Clitocybe adirondackensis	TENN064660	Tennessee, USA	HQ728529	HQ728530	HQ728531	HQ728532
Clitocybe aff. *fellea*	TENN062782	Pennsylvania, USA	HQ728533	HQ728534	HQ728535	HQ728536
Clitocybe candicans	TENN062336	Massachusetts, USA	DQ202268	AY645055	AY771609	DQ385881

Clitocybe dealbata	HC95.cp3	Unknown	AF357061	AF223175	DQ825431	DQ825407
Clitocybe nebularis	PBM2259 (WTU)	Washington, USA	DQ486691	DQ457658	DQ437681	DQ470833
Clitocybe subditopoda	TENN062348	Massachusetts, USA	DQ202269	AY691889	AY771608	AY780942
Clitopilus prunulus	TJB6838 / TJB9663 (CORT)	New York, USA	DQ202272	AY700181	AY771607	GU384615
Conocybe apala as *"C. lactea"*	TENN062525	Massachusetts, USA	DQ486693	DQ457660	DQ437683	DQ470834
Conocybe smithii	**TENN068317**	**Oregon, USA**	**KF830097**	**KF830088**		**KF830068**
Coprinellus disseminatus	NCBI	Various	AY461838	AF056456		DQ056143
Coprinopsis atramentaria	PBM992 (WTU)	Washington	DQ115781	DQ457660	DQ486694	
Coprinopsis cinerea	Various		AF345819	AF041494	AFTOL-ID 1087	XM_001829088
Coprinus comatus	ECV3198 (UC)	California, USA	AY854066	AY635772	AY665772	AY780934
Cortinarius aurilicis	TSJ1998-101 (C)	France	DQ083772	AY684152	AY705957	DQ083880
Cortinarius bolaris	MB96-086 (REG)	Germany	AF389169	AY293173	AY293125	
Cortinarius iodes	TENN062303	Massachusetts, USA	AF389133	AY702013	AY771605	AY536285
Cortinarius sodagnitus	TF2001-094	Denmark	DQ083812	AY684151	AY752975	DQ083920
Cortinarius violaceus	MTS4854 (WTU)	Washington, USA	DQ486695	DQ457662	AY705950	DQ470835
Crepidotus cf. *applanatus*	PBM717 (WTU)	Washington, USA	DQ202273	AY380406	AY705951	AY333311
***Crepidotus* sp. PBM3463**	**PERTH08242135**	**Western Australia, AU**	**HQ728537**	**HQ728538**	**HQ728539**	**HQ728540**
Crepidotus variabilis	REG JE 5.3	Unknown		AY293174	AY293126	
Crucibulum laeve	REG Crul1	Unknown	DQ486696	AF336246	AF026624	DQ470836
Cyathus striatus	DSH96-028 (CUW)	Unknown	DQ486697	AF336247	AF026617	DQ472711
Cystoderma amianthinum	TENN063549	Wales, UK	GU296098	DQ154108	GU296097	
Deconica montana	PBM961 (WTU)	Washington, USA	DQ494692	DQ470823	DQ465342	
***Deconica* sp. PBM3781**	**TENN067013**	**Queensland, AU**	**KC669314**	**KF830081**	**KF830076**	**KF830064**
Descolea maculata	E8078 (PERTH)	Western Australia, AU	DQ192181	DQ457664	DQ440633	
Descolea phlebophora	**TENN063626**	**New Zealand**	**HQ728543**	**HQ728544**	**KJ137258**	**HQ728545**
Descolea recedens	**TENN063870**	**Tasmania, AU**	**HQ728546**	**HQ827174**		**HQ827175**
Descolea tenuipes	**TENN063871**	**Tasmania, AU**	**HQ832453**	**HQ832466**	**HQ832443**	**HQ832432**
Entoloma "prunuloides"	TJB4765 (CORT)	New York, USA	DQ206983	AY700180	AY665784	DQ385883
Entoloma canescens	TB5657 (CORT)	USA		AF261307	DQ851575	
Entoloma sericeum	VHAs03/02 (DUKE)	Unknown	DQ367430	DQ367423	DQ367421	DQ367435
Entoloma sinuatum	TJB5349 (CORT)	New York, USA	DQ486700	AY69189	AY657007	
Entoloma strictius	JM96/10 (DUKE)	USA	DQ494680	AF042620	AF287832	AY218483

Flammula alnicola	PBM2608 (CUW)	Tennessee, USA	DQ486703	DQ457666	DQ113916	DQ472714
Flammulaster sp. PBM1871	PBM1871 (WTU)	Washington, USA		AY380408		AY33315
***Flammulaster* sp. PBM3449**	**TENN065366**	**Tasmania, AU**	**HQ827176**	**HQ827177**	**HQ827178**	
Galerina atkinsoniana	TENN062533	Colorado	DQ486705	DQ457668	DQ440634	
Galerina clavus	**Contu15122007**	**Italy**	**HQ832447**	**HQ832461**	**HQ832429**	
Galerina clavus as *"Tubaria minima"*	PAM06090110 (LIP, epitype)	France	EF051060	EF051055		
Galerina marginata	TENN062367	Massachusetts, USA	DQ192182	DQ457669	DQ440635	
Galerina semilanceata	PBM1389 (WTU)	Washington, USA	DQ486706	AY038309	DQ440639	AY337357
***Galerina* sp. NLB00293**	**NLB00293 (PERTH)**	**Western Australia, AU**	**HQ827179**	**HQ827180**	**HQ827181**	
Gymnopilus sapineus	PBM1541 (WTU)	Wyoming, USA		AY380362		AY337358
Gymnopilus spectabilis	PBM2471 (CUW)	Massachusetts, USA	DQ4867707	AY700186	DQ440642	
Hebeloma affine	**TENN063921**	**Ontario, Canada**	**FJ436320**	EF561632	**HQ832422**	**FJ436321**
Hebeloma olympianum	BK21Nov9820 (UTC)	Washington, USA		AY038310		AY337359
Hebeloma velutipes	PBM2277 (WTU)	California, USA	AY818351	AY745703	AY752972	DQ472718
Hydnangium carneum	**TENN063868**	**Tasmania, AU**	**HQ832445**	**HQ832455**	**HQ832423**	**HQ832433**
Hymenagaricus taiwanensis	HKAS4254	Taiwan	DQ490633	DQ457680	DQ089016	
Hypholoma australe	**PERTH08241856**	**Western Australia, AU**	**HQ832446**	**HQ832456**	**KJ137259**	**HQ832434**
Hypholoma fasciculare	PBM1844 (WTU)	Washington, USA		AY380409		AY337413
Hypholoma sublateritium	JS031107 (CUW)	Massachusetts, USA	AY818349	AY635774	AY787215	
Hypholoma subviride	**TENN062712**	**Tennessee, USA**	**HQ222020**	**HQ832457**	**HQ832424**	**HQ832435**
Infundibulicybe gibba	JCS0704B (CUW)	Massachusetts, USA	DQ490635	DQ457682	DQ115780	DQ472727
Inocephalus sp. GD-b	TENN063926	Argentina	DQ490636	DQ457683	DQ457622	DQ472728
Inocybe aff. *asterospora*	TENN065796	New York, USA	DQ404390	AY702015	AY654889	
Inocybe lilacina	PBM2039 (WTU)	Washington, USA	HQ201357	AY380385		AY337388
Inocybe mutata	TENN062387	Massachusetts, USA	JQ801410	AY732212	DQ457623	DQ472729
Inocybe myriadophylla as *"I. dulcamara"*	JV19652F (TUR-A)	Finland	DQ221106	AY700196	AY657016	AY803751
Inocybe rimosoides as *"I. cookei"*	PBM2459 (CUW)	New York, USA	DQ404391	AY702014	AY752967	DQ385884
Inocybe unicolor	PBM1841 (WTU) / RV7/4 (DUKE)	Missouri, USA	EU523554	AY380403	AF287836	AY337409
Kuehneromyces rostratus	TENN062522	Massachusetts, USA	DQ490638	DQ457684	DQ457624	DQ472730
Laccaria amethystina	DSH s.n. (CUW)	Unknown		AF393062	AF287837	
Laccaria bicolor	Varioius		DQ149869	AF042588		XM_001873347

Laccaria ochropurpurea	TENN062315	New York	AF006598	AY700200	AY654886	DQ472731
Laccaria pumila	DSH s.n. (CUW)	Unknown		AF287869	AF287838	
Lacrymaria velutina	TENN062313	Massachusetts, USA	DQ490639	AY700198	AY654885	DQ472733
Langermannia gigantea	DSH96-032	Unknown		AF518603	AF026622	
Lepiota cristata	ECV2449 (UC)	Michigan, USA	AF391041	DQ457685	DQ457627	
Lepiota maculans	**TENN064381**	**Tennessee, USA**	HM222929	**HQ832458**	**HQ832425**	**HQ832436**
Lepista irina	PBM2291 (WTU)	Washington, USA	DQ221109	DQ234538	AY705948	DQ385885
Lepista personata	**TENN066100**	**Tennessee, USA**	**KJ137270**	**KJ137271**	**KJ137260**	
Lepista sordida	**CRG014 (TENN)**	**Tennessee, USA**	**KJ137272**	AY207225	**KJ137261**	**KJ137273**
Leucoagaricus barssii	ECV3126 (UC)	California, USA	DQ911600	DQ911601	GU187658	DQ911602
"*Leucopaxillus albissimus*" (=*Tricholoma* sp.)	SAR1/2/90 (DUKE)	Unknown		AF042592	AF287839	
Lycoperdon pyriforme	DSH96-054 (CUW)	Unknown	AY854075	AF287873	AF026619	AY218495
Lyophyllum* aff. *decastes	**TENN063624**	**Tennessee, USA**	**HQ832451**	**HQ832459**	**HQ832425**	**HQ832437**
Lyophyllum decastes	JM87/16	Unknown	AF357059	AF042583	DQ367419	DQ367433
Lyophyllum sp. PBM2688	TENN062511	Massachusetts, USA	DQ182502	DQ094785	DQ457628	
Macrolepiota dolichaula	HKAS31464	China	DQ221111	DQ411537	AY771602	DQ385886
Macrolepiota procera	DSH96-038	Unknown	AY243589	AF518628		
Mycocalia denudata	**CBS494.85**	**Canada**	DQ911596	DQ911597	DQ911598	**KJ137274**
Mythicomyces corneipes	PBM1210 (WTU)	Washington, USA	DQ404393	AY745707	DQ092917	DQ408110
"*Naematoloma*" *longisporum*	TENN062558	Massachusetts, USA	DQ490634	DQ457681	DQ457681	
Nidula niveotomentosa	**CBS250.84**	**Canada**	DQ917654	DQ986295	GU296099	**KJ137275**
Nivatogastrium nubigenum	PBM504 (WTU)	California, USA	DQ494679	DQ470815	DQ459373	
Ossicaulis lignatilis	DAOM188196	Unknown	DQ825426	AF261396	AF334923	DQ825410
Pachylepyrium carbonicola	PBM2293 (WTU)	Washington, USA		DQ986294		
Pachylepyrium carbonicola	**PBM1411 (WTU)**	**Washington, USA**				**HQ832438**
Pachylepyrium carbonicola	**TENN028784**	**Idaho, USA**	**HQ222013**	**HQ832460**	**HQ832427**	
Pachylepyrium carbonicola	**TENN028785**	**Idaho, USA**	**HQ222014**	**HQ222015**	**HQ832428**	
Pachylepyrium carbonicola	**AHS44640 (MICH, holotype, *Kuehneromyces carbonicola*)**	**Idaho, USA**	**HQ222012**			
Pachylepyrium fulvidula	**Okada170163 (MICH)**	**Argentina**	**KF830092**	**KF830087**		

Pachylepyrium fulvidula	**T1495 (MICH, isotype of *Phaeomarasmius fulvidulus*)**	**Argentina**	**KF830091**	**KF830080**	**KF830072**	**KF830063**
Pachylepyrium funariophilum	**IB 1949/0022**	**Austria**	**KF830095**	**KF830085**		
Pachylepyrium funariophilum	**IB 1949/0008 (holotype of *Pholiotina funariophila*)**	**Austria**	**KF830096**	**KF830086**		
"*Pachylepyrium funariophilum*" (=*Deconica* sp.)	**TENN051714**	**North Carolina, USA**	**HQ728541**	**HQ728542**	**KJ137262**	
"*Pachylepyrium funariophilum*" (=*Psilocybe* sp.)	TENN053270	Washington, USA		AF261513		
Pachylepyrium nubicola	**K(M) 181790 (holotype)**	**Venezuela**	**KF871789**			
Panaeolina foenisecii	J152 (DUKE)	Unknown		AF041537	DQ851578	
Panaeolus papilionaceus	**RN050113 (TENN, homokaryotic culture)**	**Florida**	**KF830093**	**KF830082**	**KF830073**	**KF830065**
Panaeolus sphinctrinus	PBM2009 (WTU)	Washington, USA	DQ182503	DQ470817	DQ459375	
Phaeocollybia festiva	PBM2366 (WTU)	Norway	DQ494682	AY509119	DQ462516	AY509118
Phaeomarasmius proximans	PBM1936 (WTU)	Vermont, USA	DQ404381	AY380410	AY752970	AY333314
Phaeomyces dubiosus	**TENN063604**	**France**	**KF830099**	**KF830089**	**KF830077**	**KF830070**
Pholiota* aff. *astragalina	**TENN062733**	**Tennessee**	**HQ832448**	**HQ832462**	**KJ137263** **KJ137264**	**HQ832439**
Pholiota multicingulata	**TENN063875**	**New Zealand**	**HQ832449**	**HQ832463**	**HQ832430**	**HQ832440**
Pholiota squarrosa	TENN062547	Colorado, USA	DQ494683	DQ470818	DQ465337	
Pholiotina filaris	PBM2697 (CUW)	Massachusetts, USA	DQ494684	DQ494684	DQ465338	
Pleuroflammula flammea	MCA339 (VPI)	Unknown	DQ494685	AF367962	DQ089021	DQ474124
Pleuroflammula praestans	**PERTH08242151**	**Western Australia, AU**	**HQ832450**	**HQ832464**	**HQ832431**	**HQ832441**
Pleuroflammula tuberculosa	**PAM02072903 (LIP)**	**France**	**HQ832452**	**HQ832465**	**KJ137265**	**HQ832442**
Porpoloma sp. PR3995	PR3995 (DUKE)	Puerto Rico	EF421106	AF261395		EF421013
Psathyrella candolleana	JCS0804A (CUW)	Massachusetts, USA	DQ494689	DQ110874	DQ465339	
Psathyrella gracilis	J130 (DUKE)	Unknown		AF041533	DQ851582	
Psathyrella rhodospora	MP133 (MIN)	Minnesota, USA	DQ267129	AY645058	DQ089018	
Psathyrella spadicea	PBM2710 (CUW)	Colorado, USA	DQ494690	DQ470822	DQ465340	
Pseudoclitocybe cyathiformis	JFA12811 (WTU)	Washington, USA	GU187553	EF551313	GU187659	GU187815

Psilocybe caerulipes	**TENN064502**	**Tennessee, USA**	KC669282	**KF830084**	**KF830075**	**KF830067**
Psilocybe cubensis	**DNA2052 (TENN)**	**Unknown**	**KF830094**	**KF830083**	**KF830074**	**KF830066**
Psilocybe cyanescens	**DNA1938 (TENN)**	**Unknown**	**KJ137276**	**KJ137277**	**KJ137266**	**KJ137278**
"*Psilocybe silvatica*"	RV5/7/1989		AY129362	AF042618	DQ851583	
Psilocybe stuntzii	VT1263	Unknown		AF042567	DQ851584	
Psilocybe subaeruginosa	**TENN065481**	**Tasmania, AU**	KC669728	**KF830079**	**KF830071**	**KF830062**
Rhodocybe mundula	TJB7599 (CORT)	New York, USA	DQ494694	AY700182	DQ089017	DQ474128
Simocybe serrulata	TENN062382	Massachusetts, USA	DQ494696	AY745706	DQ465343	DQ484053
***Simocybe* sp. PBM3031**	**TENN062784**	**Tennessee, USA**	**GQ893023**	**GQ892979**	**KJ137267**	**HQ832444**
Squamanita paradoxa	TENN063549	Wales, UK	GU296096	EF535266	GU296095	
Stropharia ambigua	PBM2257 (WTU)	Washington, USA	AY818350	AY646102	DQ092924	DQ484054
Tephrocybe boudieri	BSI96/84	Unknown	DQ825427	DQ825430	DQ825433	DQ825411
Termitomyces microcarpus as "*Podabrella microcarpus*"	PRU3900	Unknown		AF042587	DQ851581	
Termitomyces sp. ZA164	ZA164	South Africa	DQ494698	DQ110875	DQ092922	DQ437070
Tricholoma inamoenum	MB96-071 (REG)/ KMS249	Unknown/California	AF377246	AY293215	AY293161	
Tricholoma matsutake	Unknown	Unknown	U62964	U62964	U62538	
Tricholoma myomyces	KMS589	Unknown	DQ825428	U76459	DQ367422	DQ367436
Tricholoma palustre as *"T. aestuans"*	PBM2494 (CUW)	Massachusetts	DQ494699	AY700197	AY757267	DQ484055
Tricholoma saponaceum	PBM2514 (CUW)	Massachusetts	DQ494700	AY647209	AY654883	
Tricholomella constricta	HC84_75	Unknown	DQ825429	AF223188	DQ825434	DQ825412
Tubaria confragosa	PBM2105 (WTU)	Washington, USA	DQ267126	AY700190	AY665776	DQ408113
Tubaria furfuracea	MCA391 (VPI)	California, USA	AF205710	DQ851587	DQ851587	
Tubaria serrulata	E8069 (PERTH)	Western Australia, AU	DQ182507	DQ156128	DQ462517	
***Tubaria* sp. BM378_17**	**TENN063912**	**Washington, USA**	**HQ832454**	**HQ832467**	**KJ137268**	**HQ839738**
***Tubaria* sp. PBM3355**	**TENN065365**	**Tasmania, AU**	**HQ839739**	**HQ839740**	**HQ839741**	
Tubaria vinicolor	JFA12905 (WTU)	Washington, USA	DQ536417	DQ536415	DQ536416	DQ536418
Tulostoma macrocephala	Long 10111 (FH)	Unknown		AF518663	AF026625	
undet. Agaricaceae RC_Mart06_016	**RC_Mart06_016 (LIP)**	**Martinique**	**HQ839742**	**HQ839743**	**HQ839744**	**HQ839745**
undet. Bolbitiaceae PBM3032	**PBM3032 (TENN)**	**Tennessee, USA**	**HQ840656**	**HQ840657**	**KJ137269**	**HQ840658**
undet. Hymenogastraceae PBM3116	**PBM3116 (TENN)**	**New Zealand**	**HQ840659**	**HQ840660**	**HQ840661**	**HQ840662**

undet. Hymenogastraceae PBM3420	**PBM3420 (TENN)**	**Tasmania, AU**	**HQ840663**	**HQ840664**	**HQ840665**	**HQ840666**
Verrucospora flavofusca	HKAS41933	China	DQ241779	DQ470825	AY665783	

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